Section 6: Effect of cognitive factors on sensorimotor activation: Attention to somatosensory stimulation

Activity in sensorimotor regions reflects not only movement or sensation parameters but also cognitive factors (Georgopoulos 2000). Hence, activity is seen in motor cortex during motor imagery (Porro et al. 1996) and in somatosensory cortex during anticipation of touch (Drevets et al. 1995). Furthermore changes in sensorimotor representations are seen during motor learning (Karni et al. 1995) or tactile learning (Recanzone et al. 1992). It is likely that patients whose movement has been affected by stroke would differ from healthy controls in cognitive aspects of movement, as well as in the simple production of motor output. In particular, it is possible that patients may pay more attention to their movements than controls. If attention modulates activity in sensorimotor regions then this factor would be of relevance to clinical studies of motor recovery. I therefore tested the hypothesis that attention to touch (this section) and attention to movement (Section 7) modulate processing in somatosensory and motor cortices in normal subjects.

6.1   Introduction and rationale

6.1.1   Attentional networks in the brain

After decades of research on selective attention, one of the clearest definitions of attention is still to be found in William James's *Principles of Psychology*, written in 1890.

"Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others."(James 1890)

It is this ability which allows us to attend to one conversation in a crowded room, blocking out all other noise. This voluntary or 'top-down' focussing of attention is distinct from the reflexive or 'bottom up' shifting of attention that occurs when we hear our name in another, unattended conversation. The cocktail party scenario illustrates some of the main issues in attentional research. For example – does selective attention to one input lead to increased sensitivity to the attended input? Does the presence of competing conversations affect processing of the attended input? To what level are unattended stimuli processed?

This last question is of interest both from the psychological point of view (e.g. is an unattended word processed to the level of phonology or to the level of semantics?) and from the physiological point of view (e.g. does attention operate at the level of the peripheral receptors, primary sensory cortex, secondary sensory cortices or all levels?).

Most studies of selective attention have focussed on the visual system (Posner *et al.* 1982; Corbetta *et al.* 1991; Motter 1993). It is known that selectively attending to a location in space enhances our perception of visual stimuli appearing at that location (Posner *et al.* 1982) and that this behavioural advantage has neural correlates (Motter 1993). However, far fewer studies have explored the behavioural consequences of selective attention to touch (Craig and Evans 1995; Lloyd *et al.* 1999; Whang *et al.* 1991; Sathian and Burton 1991; Horner 1995; Rinker and Craig 1994) or their neural correlates (Johansen-Berg and Lloyd 2000).

6.1.2   The behavioural correlates of selective attention to touch

James suggested that selective attention allows us to 'deal effectively' with the attended stimulus (James 1890). In more recent years there have been a number of studies testing the hypothesis that selective attention to touch facilitates processing of the attended stimulus. The results of such studies have been mixed. For example, in tactile versions of Posner's classic visual cueing paradigm (Posner 1978; Butter *et al.* 1989; Bradshaw *et al.* 1992) subjects are cued to expect a tactile stimulus to a particular body location. Posner cued subjects to expect a tap to either the left or right index fingertip and found no significant effect of cueing on response time (Posner 1978). However, in a similar experiment using both visual and tactile cues a significant effect of cueing was found for a tactile detection task (for both cue types), although the effect was smaller than for the analagous visual detection task

(Butter *et al.* 1989). Bradshaw et al also report significant cueing effects in a tactile detection task (Bradshaw *et al.* 1992).

6.1.3 The neural correlates of selective attention to touch – how early does modulation occur?

Many psychological models of selective attention assume that attention acts to filter out irrelevant information in order to protect our limited-capacity processing systems from information overload (Posner and Cohen 1984). However, such models vary as to whether they place the attentional filter early or late in a processing stream.

It was established in Section 1.2.2 that in monkeys and arguably in humans, the neural pathways for touch processing are organised serially, with the main projections going from the ventroposterior thalamus to S1 then from S1 on to S2 and other association areas (Pons *et al.* 1987). The issue of how early the attentional filter operates in touch can be addressed by determining the degree of attentional modulation at different stages along this pathway.

This question has been extensively studied in the visual system (Corbetta *et al.* 1991; Motter 1993; Watanabe *et al.* 1998; Brefczynski and DeYoe 1999). It is now widely accepted that attention modulates extrastriate visual areas (Corbetta *et al.* 1991) and that attentional effects can be seen in the primary visual cortex in certain conditions (Motter 1993; Watanabe *et al.* 1998; Brefczynski and DeYoe 1999). However, a number of studies have shown that the effects are larger (Kastner *et al.* 1998) and occur earlier (Martinez *et al.* 1999) in extrastriate areas than in the primary visual cortex. Attentional effects have also been demonstrated in the auditory system. However in contrast to the findings for the visual system, a recent FMRI study reported greater attentional modulation of primary than secondary auditory cortex (Jancke *et al.* 1999).

Attentional modulation of somatosensory regions has been demonstrated using single unit recording in monkeys (Hsiao *et al.* 1993; Hyvarinen *et al.* 1980; Iriki *et al.* 1996), SEPs (Desmedt and Tomberg 1989; Garcia *et al.* 1992; Bruyant *et al.* 1993), MEG (Mima *et al.* 1998; Mauguiere *et al.* 1997) and PET (Roland *et al.* 1982; Drevets *et al.* 1995; Burton *et al.* 1999; Meyer *et al.* 1991). Although a number of these studies have reported attentional modulation of S1 (Roland *et al.* 1982; Meyer *et al.* 1991), some studies have found that S1 is not modulated by attention (Mima *et al.* 1998; Mauguiere *et al.* 1997) or is modulated to a lesser degree than S2 (Burton *et al.* 1999; Hsiao *et al.* 1993). Determining the level in the somatosensory system at which modulation occurs is important for understanding attentional processes. In the context of this thesis, determining which somatosensory cortical areas show attentional modulation will help us assess the degree to which altered attention to sensory input or movement might explain the changes in activation patterns seen with movement of the affected hand after stroke.

The present study used quantitative analysis of the BOLD (Blood Oxygenation Level Dependent) FMRI response to investigate attentional modulation of primary and secondary somatosensory areas. A comparison was made between activation during somatosensory and visual target detection tasks, with both stimulus types present in both tasks. Attentional effects were quantified using two different approaches to analysis: a random effects analysis based on the group data, and a comparison of the maximum signal changes for attended and unattended touch for each subject within regions of interest defined by neuroanatomical landmarks on the individual brains.

6.2　Methods

Subjects 9 right handed healthy subjects (4 female, 5 male, aged 20-35) participated. Subjects gave informed consent in accordance with ethical approval from the Central Oxford Regional Ethics Committee.

FMRI scanning A 3T Varian INOVA MRI system with a multislice gradient echo EPI sequence was used (TR=3000ms, TE=30ms, flip angle=90°, FOV=256mm^2, matrix=64^2, 21 6mm axial slices). A high-resolution T1-weighted anatomical scan was also acquired for each subject (IR 3D Turbo Flash, 64x3mm axial slices, TR=30ms, TE=5ms, TI=500ms, flip angle=15°, FOV=256x256, matrix=256x256).
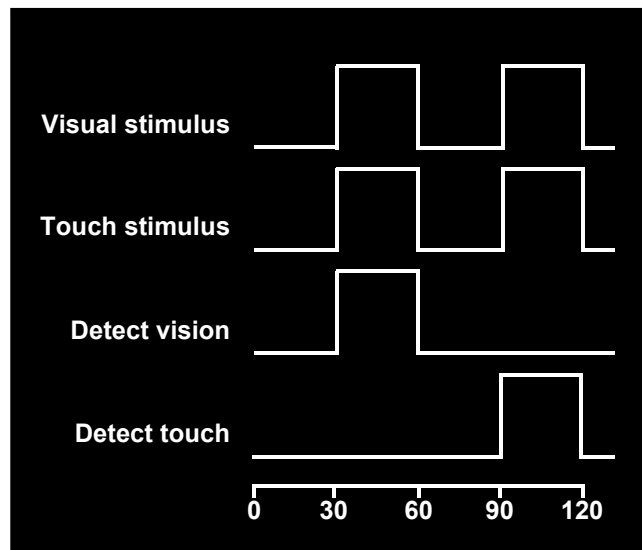

Figure 6.1: Paradigm design: One ABAC cycle. This cycle was repeated 3 times giving a total experiment length of 6 minutes. Both visual and touch stimuli were present in each task block but subjects were instructed to attend either to the visual stimulus (by the word "screen") or the touch stimulus (by the word "toe")

The paradigm consisted of alternating 30 second periods of task and rest (Figure 6.1). The tasks alternated between visual and somatosensory target detection. Both tasks required the subject to press a button with the right index finger as quickly as possible after the appearance of the target stimulus. The target modality was indicated at the beginning of each task period by the appearance of the word 'toe' or 'screen' on the visual display, viewed

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through prism glasses. The visual stimulus was a red and white checkerboard. The touch stimulus was applied to the subject's left great toe with a plastic rod that delivered a constant pressure. The touch and visual stimuli were delivered at different times and on average once a second. The inter-stimulus interval was varied randomly between 0.5 and 1.5 seconds to minimise anticipatory responses.

Reaction times were measured to confirm that subjects were attending during the visual detection task, but this could not be tested directly during the somatosensory detection task as the timing of the manually-delivered somatosensory stimuli was not measured. Subject reports after each session were therefore used to confirm that subjects felt they performed both touch and visual target detection tasks adequately.

Image Analysis Image analysis was performed within MEDx (Sensor Systems, Inc., VA, USA). For each subject, automated image preprocessing and t-tests were carried out using FEAT 2.0 (FMRIB, Oxford, UK). This included motion correction using the SPM realign procedure with adjustment for movement (Friston *et al.* 1995), spatial smoothing using a Gaussian kernel of FWHM 5mm, global (volumetric) multiplicative mean intensity renormalization, matched-Gaussian/Butterworth bandpass filtering of lowpass HWHM 2.8s and high pass period 180.0s. T-tests were performed to test for changes between attended and unattended touch conditions, and between touch conditions and rest. These generated Gaussianised t-statistic (Z statistic) images and mean difference images. The mean difference images for each subject were warped into a standard brain space (Talairach and Tournoux 1988) using FMRIB's Linear Image Registration Tool (FLIRT, FMRIB, Oxford, UK) and used in random effects analyses (Holmes and Friston 1998) to generate group Z statistic images. Cluster detection was applied to the group Z statistic images (Z>2.3, p<0.1) (Friston *et al.* 1992; Worsley *et al.* 1992; Forman *et al.* 1995).

Volumes of interest covering primary and secondary somatosensory cortices and somatosensory insula were defined for each subject based on their anatomical scan as follows (Figure 6.2):

1. Primary somatosensory cortex (S1): The toe area was defined as the cortex on the medial wall of the contralateral (right) hemisphere posterior to the central sulcus and anterior to the postcentral, sulcus extending from the dorsal surface of the brain to the upper margin of the cingulate sulcus (Penfield and Boldrey 1937)

2. Secondary somatosensory cortex (S2): Volume including the upper bank of the sylvian fissure from the most posterior point of the fissure anteriorly for 2 cm, from the most dorsal margin of the fissure ventrally for 2 cm, and from the medial margin laterally for 2 cm (Maeda *et al.* 1999).

3. Insular cortex: The insula has been shown to be activated by touch, but has not been demonstrated to have somatotopic specialisation, so the insular VOI included the whole of the insular cortex (Burton *et al.* 1993).
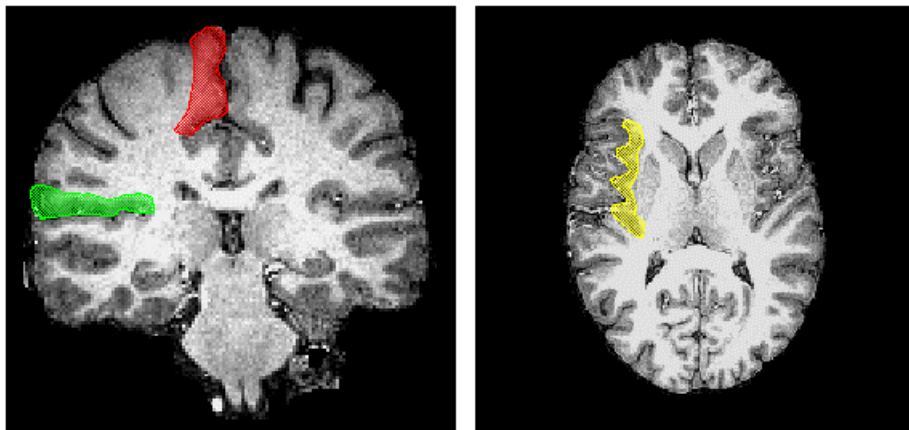

Figure 6.2: Illustrative example of volumes of interest drawn on a single subject's high resolution T1-weighted scan. **Red:** primary somatosensory cortex; **Green:** Secondary somatosensory cortex; **Yellow:** Insular cortex

The VOIs were registered in EPI space using FLIRT (Jenkinson and Smith 2001) (FMRIB, Oxford, UK) and applied to the signal change images comparing activation

conditions to rest. For attended touch versus rest and for unattended touch versus rest, the voxel with the maximum percent signal change was identified and the mean signal intensity time course of this voxel was extracted. The mean time course for each subject was normalised using the average of the four scans before each task period as a baseline which was set to an arbitrary value of one thousand.

One-tailed Wilcoxon signed ranks tests were used to determine whether the group showed a greater maximum signal change in somatosensory areas from rest to touch when the touch was attended.

6.3 Results

Overall, the results demonstrate that attention to touch modulates activity in somatosensory areas including S1. One aim of the study was to compare two analytical approaches: a group random effects and an individual subject regions of interest analysis. The attentional effect in primary somatosensory cortex was revealed only with the regions of interest approach. Results from the two approaches and possible reasons for discrepancies between them are discussed in detail below.

Significant activation was detected in primary and secondary visual and somatosensory cortices for both detection tasks versus rest for all subjects (Table 6.1).

Task	Anatomical region	Talairach co-ordinates of cluster centres			Pixel count	P
		x	y	z		
Visual target detection versus rest	Left motor cortex	-40	-21	53	23900	<0.001
	Bilateral V1 plus extrastriate areas	7	-83	1	17130	<0.001
	SMA	2	7	54	5743	<0.001
Touch target detection versus rest	Left motor cortex extending down into left insula	-42	-15	38	47450	<0.001
	Right S2	58	-39	13	19170	<0.001
	Right insula	41	1	32	16426	<0.001
	SMA extending posteriorly to include S1	5	-2	62	8962	<0.001
	Left S2	-49	-59	8	2724	0.07

Table 6.1: Activated clusters (Z>2.3 p<0.1) in random effects group analysis of target detection versus rest

The effect of attention to touch was tested first by performing the random effects group analysis comparing the somatosensory target detection task to the visual target detection task (both visual and somatosensory stimuli were present throughout both tasks). This revealed three clusters of activation (Figure. 6.3, Table 6.2). A large cluster in the right hemisphere (contralateral to the touch) included both the secondary somatosensory cortex and the lateral edges of the insula, including the circular insular sulcus (6194 pixels, $p=0.001$). In the left hemisphere one cluster included the secondary somatosensory cortex (3672 pixels, $p=0.03$) and another covered the insular cortex (3224 pixels, $p=0.06$). The random effects analysis did not reveal significant attentional effects in the primary somatosensory cortex.

Anatomical region	Talairach co-ordinates of cluster centres			Pixel count	P
	x	y	z		
Right S2 and insula	59	-14	10	6194	0.001
Left S2	-52	-17	20	3672	0.029
Left insula	-44	8	13	3224	0.055

Table 6.2: Activated clusters (Z>2.3, p<0.1) in random effects analysis of attended vs unattended touch.

The random effects analysis is a strict test as it requires not only that a large proportion of subjects show an effect, but also that after registration of activation images from the individual subjects, the loci of that effect from the different subjects overlap in the standard brain space. The failure to detect enhanced activation with attention in contralateral S1 using the random effects model could therefore arise if S1 showed a small volume of activation relative to S2, a greater variance in signal change, or less attentional modulation.
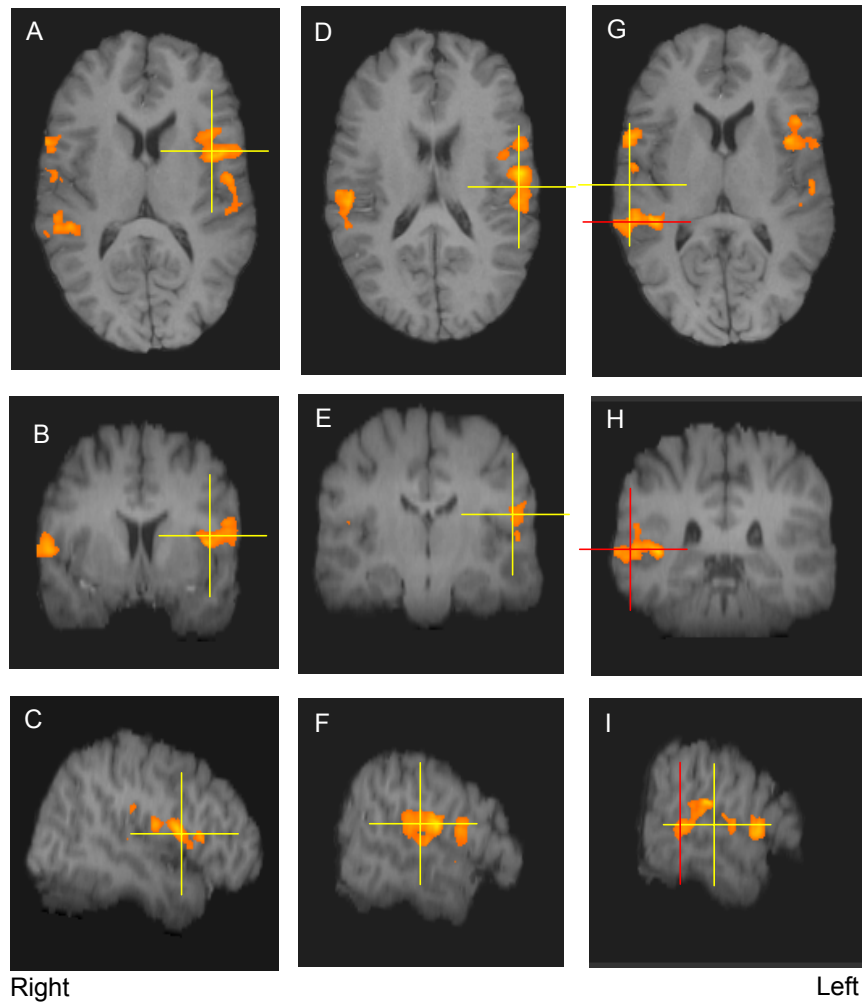
Figure 6.3: A comparison of attended versus unattended touch revealed clusters in bilateral insula and secondary somatosensory cortex (S2). The left insula cluster is seen in A (axial), B (coronal) and C (saggital) (crosshairs are at cluster centre, see Table 2). The left S2 cluster is seen in D, E and F. Activation in the insula and in S2 was bilateral as can be seen in the axial views in D (for S2) and A and G (for insula). In the right hemisphere the insula and S2 activations are joined to form a single cluster whose centre is indicated by the yellow crosshairs in G and I. The position of the right S2 activation can be seen in H which is a coronal slice taken at the position marked by the red lines in G and I. The position of the insula activation differed between the left and right hemispheres (see A,B,G): in the left hemisphere activation was in the insular cortex itself whereas in the right hemisphere activation was more lateral, along the circular insular sulcus and towards the sylvian fissure.

Each of these possibilities was explored in turn. 8/9 subjects activated a greater number of pixels in contralateral S2 than in S1 (Table 6.3, Z=-2.2, p=0.03). In addition, the variance of signal change measurements from S1 was substantially greater than for S2 (e.g., attended touch vs rest: mean maximum signal change contralateral S1 = 0.8 ± 0.7%; contralateral S2 mean = 0.6 ± 0.2%; also see Figure 6.5).

Subject	Right S1	Right S2
1	13	71
2	10	71
3	4	6
4	2	57
5	4	92
6	8	12
7	19	7
8	10	11
9	12	25

Table 6.3: Number of significantly activated voxels for contralateral S1 and S2 after Bonferroni correction (p<0.05) within VOIs.

To allow for individual variation in the location and magnitude of response in S1, an additional analysis was performed based on signal change in volumes of interest defined by anatomical landmarks on the individual brains. For each subject, the pixel with the maximum percent signal change between activation and rest was identified for both the attended and the unattended touch conditions (Figure 6.4). The time course of the normalised signal intensity of these pixels was extracted (Figure 6.5). The maximum signal change from rest was greater for attended than for unattended touch in the toe area of right S1 for 7/9 subjects (one-tailed Wilcoxon signed ranks test, Z=2.19, p=0.01). Significant effects were also found in right S2 (8/9 subjects, Z=2.19, p=0.01). A similar trend was seen

in right insula (6/9 subjects, Z=1.72, p=0.04), left insula (8/9 subjects, Z=1.72, p=0.04) and left S2 (6/9 subjects, Z=1.48, p=0.07).

The relative magnitude of the attentional effect in S1 and S2 was compared by testing the difference between signal changes in the attended and unattended conditions in these areas. 6/9 subjects showed a larger difference in S1 than S2, but this difference was not significant (two-tailed Wilcoxon signed ranks test, Z=0.533, ns).
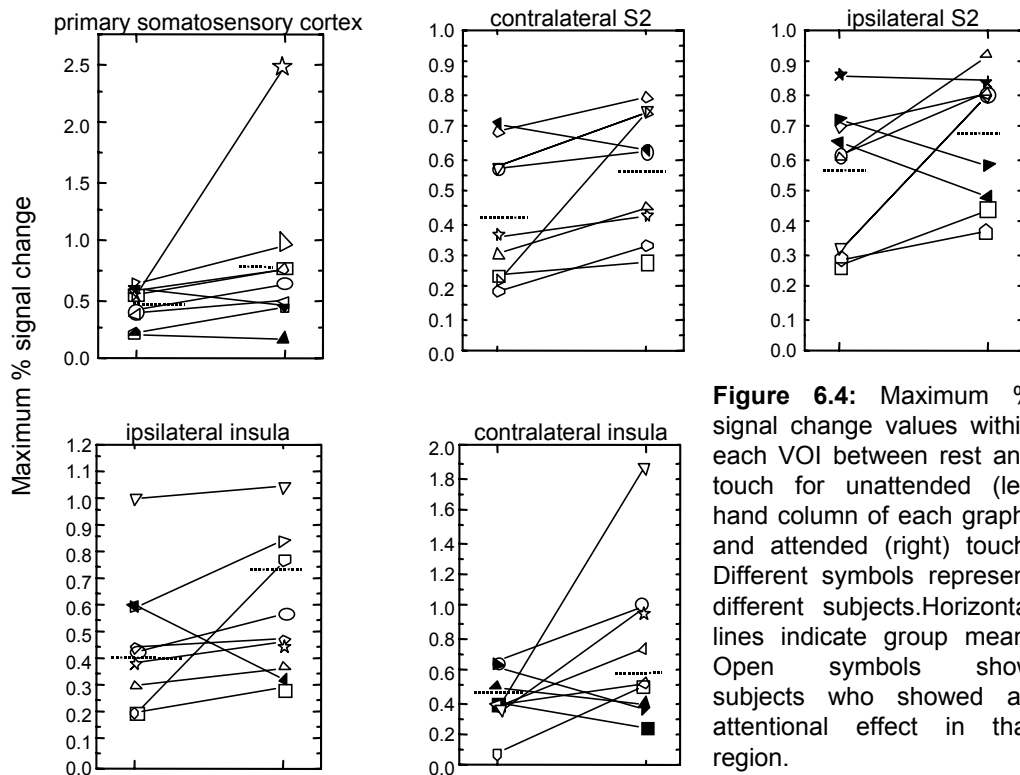

Figure 6.4: Maximum % signal change values within each VOI between rest and touch for unattended (left hand column of each graph) and attended (right) touch. Different symbols represent different subjects. Horizontal lines indicate group mean. Open symbols show subjects who showed an attentional effect in that region.
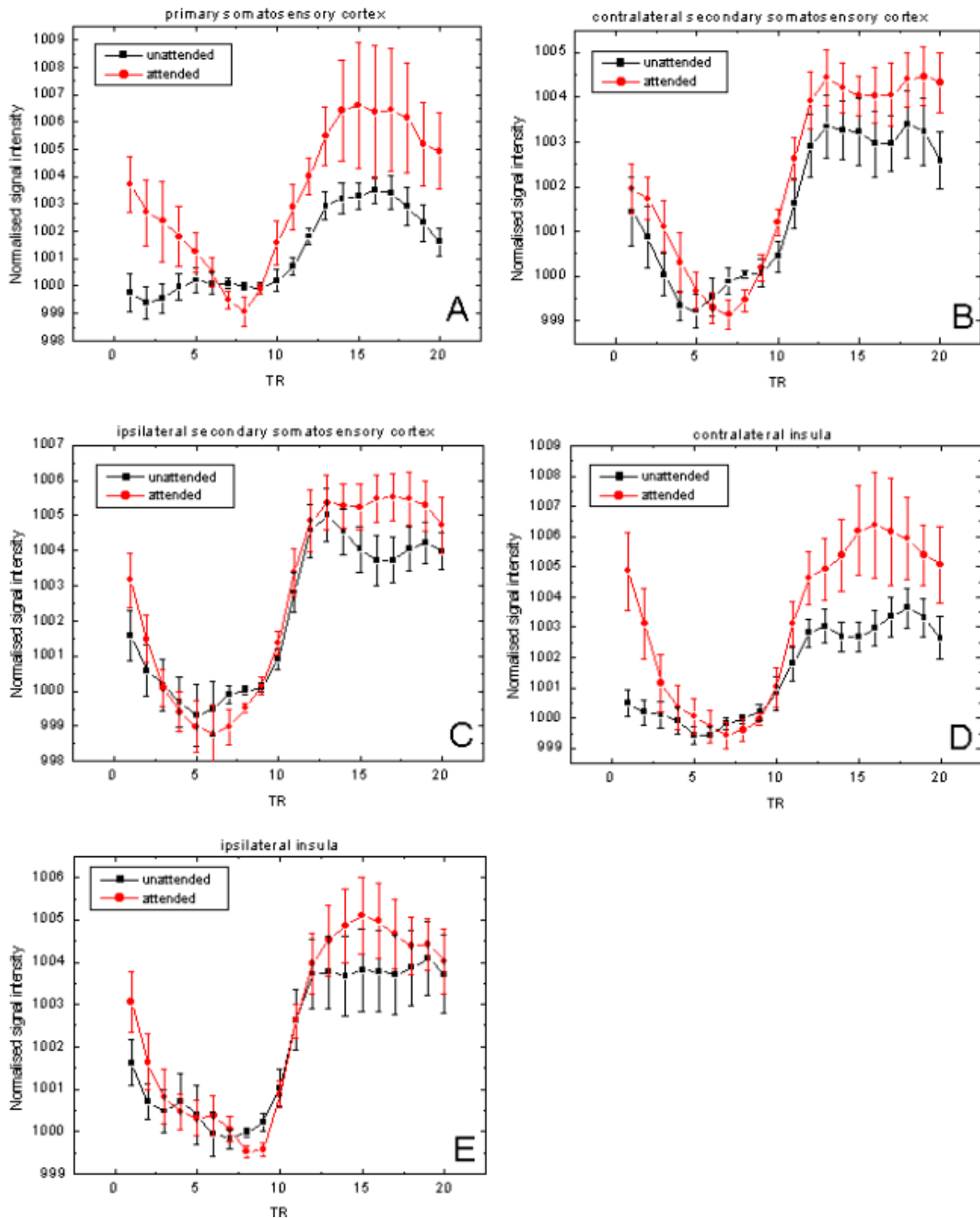
Figure 6.5: Mean time course of normalised signal intensity for pixel with maximum signal change within each VOI. Normalised intensity values for rest and touch conditions have been averaged for each subject, then all subject's mean values have been averaged to find the group time course. TRs 1-10 are rest periods and TRs 11-20 are touch periods. The black lines represent unattended touch and the rest period preceding it. The red lines represent attended touch and the rest period preceding it. Error bars are standard errors of group means. (The signal appears to rise during the rest period in some areas. This may reflect recovery from the "post-stimulus undershoot" that is typically seen after stimulation).

6.4　Discussion

6.4.1　Summary of findings

This experiment has shown that directing attention to a tactile stimulus results in increased activation in somatosensory cortical areas including S1. Contrary to some previous reports (Mima *et al.* 1998; Burton *et al.* 1999), there was no evidence for greater attentional effects in contralateral S2 than S1. In fact, the mean difference in maximum percentage signal change between attended and unattended touch was greater for primary somatosensory cortex than for contralateral S2 for 6/9 subjects, consistent with findings for attended sound in auditory cortex (Jancke *et al.* 1999) but in contrast to results from the visual system (Kastner *et al.* 1998; Martinez *et al.* 1999).

This demonstration of attentional modulation of primary somatosensory cortex adds to a growing body of evidence suggesting that "lower" sensory processing areas are affected by processes that are often considered to be high level such as attention (Motter 1993; Jancke *et al.* 1999; Recanzone *et al.* 1993; Xerri *et al.* 1998). This suggests that such areas operate in a dynamic rather than a "hardwired" or inflexible fashion.

There was evidence for a bilateral effect of attention in secondary but not primary somatosensory cortices. This is consistent with previous reports that touch is represented bilaterally in secondary sensory areas (Schneider *et al.* 1993; Maldjian *et al.* 1999; Robinson 1973). Bilateral attentional effects were also detected in the insula. Despite having an established role in somatosensory processing (Hsiao *et al.* 1993; Burton *et al.* 1993), the insula has received little consideration in studies of attention to non-nociceptive touch. These results showed a tendency for modulation of bilateral insula activation by attention to touch, but these effects were not as robust as those for S2 or S1.

6.4.2   Factors influencing detection of S1 modulation

There are certain features of this experiment that may account for the results demonstrating a large attentional effect in S1. First, an active distractor task (visual target detection) was used in the unattended touch condition. This may have allowed more control over the subjects' attentional state. It is possible that use of active distraction (rather than simply instructing subjects to ignore a touch stimulus) is necessary to reveal attentional modulation of S1 activation. For example, one of the earliest studies of the neural correlates of selective attention to touch was an electrophysiological study of S1 responses whilst monkeys were instructed to attend to or ignore vibration to the hand (Hyvarinen *et al.* 1980). Hyvarinen et al found that only 16% of recorded S1 cells showed increased activity levels when attention was directed towards the vibration stimulus. By contrast, a later electrophysiological study by Hsiao et al (Hsiao *et al.* 1993) found that 50% of S1 cells increased their activity with attention. One of the differences between the two studies was that the animals in the Hsaoi et al experiment were given an active distractor task (to detect the dimming of a visual stimulus) in the no attention condition.

The importance of this difference in design is highlighted by a PET study which compared S1 activation in conditions of attended touch, unattended touch and active distraction from touch (Meyer *et al.* 1991). The following conditions were used:

Unattended touch: Vibrotactile stimuli were delivered to the fingertips but subjects were not required to attend to the stimulation.

Attended touch: The same stimulation was provided and subjects were instructed to detect changes in stimulus frequency, pressure or sweeping pattern (no such changes actually occurred).

Active distraction from touch: Subjects received the same vibrotactile stimulation but were required to perform a concurrent mental arithmetic task.

All conditions produced robust activation of S1. No significant differences in S1 activation were seen between unattended (condition 1) and attended (condition 2) touch. However, attended touch did produce significantly more S1 activation than the distraction condition (condition 3). This supports the idea that active distraction helps in the detection of attentional modulation of S1. However, there was a tendency for a greater blood flow increase from the rest baseline to the attention condition (33%) than from rest to the unattended touch condition (27%) (cf 20% from rest to active distraction condition) but this difference did not reach significance. So it is not the case that distraction is necessarily different from 'no attention', but more that the addition of a distracting task allows the experimenter more control over the subject's attentional focus. This reduces the chance of the subject attending to the touch in spite of instructions not to and can reduce inter-subject variability and therefore increase the chances of detecting an effect.

Taken together with the current study, this suggests that attentional modulation can occur in S1, and that the likelihood of detecting such modulation increases when the subject is distracted from the touch stimulus in a controlled way during non-attention conditions.

6.4.3   Differential modulation of S2 versus S1?

The question still remains of whether attentional modulation occurs to *different degrees* at different levels of the somatosensory processing hierarchy. As well as studying cellular responses in S1, Hsiao et al (1993) also investigated responses in S2. They found that 80% of recorded S2 cells changed their activity with attention, compared to 50% in S1. This suggests that S2 is subject to greater attentional modulation than S1.

A number of human imaging experiments have compared the magnitude of attentional effects in S2 and S1. Using MEG, Mima et al (1998) asked subjects to perform a rare stimulus detection task (Mima *et al.* 1998). Subjects were given repetitive electrical stimulation of the median nerve. Stimuli could be either strong or weak. One stimulus type occurred 90% of the time and the other type occurred 10% of the time (in one experiment the strong stimulus was rare and in a second experiment the weak stimulus was rare). In an "active attention" condition subjects were told to mentally count the rare stimuli. In an ignore condition subjects watched a video and were not required to attend to the touch stimuli. Early responses (20–60ms) to touch stimuli that occurred over the left central area were thought to originate in S1. Later responses (100-200ms) which were maximal over bilateral temporal-parietal areas were assumed to come from S2. All responses were affected by stimulus intensity as expected. Both S1 and S2 showed response increases with stimulus deviance in both tasks, suggesting that activity in both areas is affected by reflexive or pre-attentive processes. Voluntary or active attentional processes were examined by comparing MEG responses between the two tasks. This comparison showed that only S2 showed differential responses between the two tasks, with greater response seen to the touch stimuli when they were attended.

A recent PET study by Burton (1999) et al also explored the differential effects of attention on primary and secondary somatosensory areas (Burton *et al.* 1999). In a selective attention condition subjects had to detect a change in stimulus roughness or duration. In a divided attention condition subjects were instructed to detect a change in either attribute. In a control condition subjects were given the same touch stimuli but instructed to ignore them and perform a distracting counting task. In somatosensory regions (including S1 and S2) no differences were found between blood flow responses to selective and divided attention

tasks. Comparing attention tasks to the distraction condition revealed a network of somatosensory areas modulated by attention. Foci within S1 showed some increase with attention but these did not reach significance with the most stringent statistical criteria. Decreases in S1 activity were seen when comparing passive stimulation conditions to rest (see below). In contralateral S2 significant increases were seen with attention and these increases were significantly greater than those seen in S1. A trend for attention-related increases was seen in ipsilateral S2 but did not reach significance. These data are consistent with those of Hsaoi et al in suggesting that selective attention modulates S2 activation more than S1 (Hsiao *et al.* 1993). Burton et al suggest that S2 might actually influence S1 activity via a descending control path (Burton *et al.* 1999).

However, in the current experiment significant attentional modulation was found in both S1 and S2 and no evidence was found for greater modulation in S2. In fact six out of nine subjects showed a larger maximum signal change in S1 than S2, though this difference was not significant. This finding is more in line with reports of attentional modulation in the auditory system where a recent study reported greater modulation of primary than secondary auditory cortex (Jancke *et al.* 1999). Interestingly, like the current study, the auditory attention study used a volumes of interest approach to analysis. In the current study it was only with the individual subject volumes of interest analysis that attentional modulation in S1 was revealed. This may be because a group analysis requires not only that many subjects show an effect but also that the locations of the effects overlap in standard space, once the individual subject data has been co-registered. The probability of overlap is increased if the area of activation is large. 8/9 subjects activated more pixels in contralateral S2 than S1. Therefore, the conditions for the random effects analysis are more easily satisfied for the secondary somatosensory areas. Burton et al (1999) also comment that these factors affect

the group analysis methods that they use. By contrast, a volume of interest analysis performed on the individual data sets allows account to be taken of differences in functional anatomy between the subjects. With this approach clear attentional effects were demonstrated in S1 which were at least as great as the effects in S2.

Comparing attentional effects in S1 and S2 helps to determine how early in the somatosensory processing system modulation occurs. To address this question it is also relevant to ask where *within* S1 attentional effects can be seen. The electrophysiological study of Hyvarinen et al found that 16% of recorded S1 cells increased their activity with attention (Hyvarinen *et al.* 1980). Most of these cells were located in area 1 and were minimal in area 3b/3a, where thalamic input is more direct (Jones 1983). The major projections of somatosensory information from the mammalian ventroposterior thalamus are sent to layer IV of area 3b. From here the information is relayed to other layers within S1 and then on to S2 and other regions of somatosensory association cortex. The attentionally modulated cells in the study by Hyvarinen et al (1980) were mainly located in layers I, II and VI of S1 rather than layer IV where the thalamic inputs are received. This suggests that there is a hierarchy of attentional effects within S1. However, this study was perhaps limited in sensitivity by the lack of a distraction task in the control condition. Moreover, small attentional effects have been reported to occur as early as the thalamus in the PET study by Burton et al discussed earlier (Burton *et al.* 1999).

6.4.4 Decreased activation to irrelevant stimuli

The current study and many of the previous brain imaging and electrophysiological studies of tactile attention have looked for *increases* in neural activity as a correlate of attention. However, attentional selection might also operate by decreasing signals evoked by irrelevant

stimuli. A PET study by Drevets et al looked at blood flow changes when different body parts were attended within the somatosensory modality (Drevets *et al.* 1995). This study found that the only changes in S1 activation associated with anticipation of a sensory stimulus were decreases in areas outside the representation of the skin areas of expected stimulation. For example when subjects were required to count stimuli to the fingertips (no such stimuli were actually delivered) there was a decrease in blood flow to the areas of S1 representing the face. Drevets et al therefore suggest a model of selective attention to touch in which "potential signal enhancement may rely on generalized suppression of background activity". In the visual system a number of studies have reported a suppressive effect of attention in extrastriate areas (Moran and Desimone 1985; Kastner *et al.* 1998) and inferotemporal cortex (Chelazzi *et al.* 1993). It is possible that both a gain in the signal evoked by the attended stimulus, and a damping down of distracting stimuli contribute to effective attentional selection. This would suggest that different populations of neurons are modulated in different directions. This is consistent with Hsiao et al's finding in S2 where 58% of cells increased their activity with attention and 22% showed a decrease in activity and with a study by Hsaio et al which reported suppression and enhancement attentional effects in S2 at different stages of a trial (Hsiao *et al.* 1993).

6.4.5   Potential mechanisms for attentional selection

Insight into the potential mechanism for attentional selection was provided by a recent electrophysiological study of S2 responses in monkeys (Steinmetz *et al.* 2000). Three monkeys were trained to perform tactile and visual tasks and to switch between modalities when instructed. Pairs of S2 cells were recorded and firing synchronicity during the tactile discrimination task was compared with that elicited by the same touch stimuli whilst the

monkeys performed a distracting visual task. The three monkeys tested performed slightly different tactile tasks. In the monkey performing the most difficult task, 35% of recorded S2 cell pairs showed a change in firing synchronicity (independent of any changes in firing *rate*) relative to the control task. Of these cells, 80% showed an increase in synchronicity and 20% showed a decrease relative to control. A computational model of attentional selection has shown that changes in synchronicity can change the efficacy of a representation and thus could underlie attentional selection (Neibur and Koch 1994). The electrophysiological study by Steinmetz et al tests the neuronal plausibility of this model and supports the intriguing possibility that changes in synchronicity, which could lead to changes in synaptic efficacy, could form the basis of attentional selection in the somatosensory system (Steinmetz *et al.* 2000).

6.4.6   Conclusions

In summary, this section has demonstrated that increased attention to touch leads to increased activity in a distributed network of somatosensory processing areas including primary somatosensory cortex. This may have implications for interpretation of clinical studies of movement after stroke. Some brain imaging studies have reported increased activity in sensory areas over the course of movement recovery (Marshall *et al.* 2000) or after passive movement training (Nelles *et al.* 2001). As these same areas are modulated by attention, it would be useful to assess the degree to which changes in attentional focus occur after stroke. This could help determine whether the altered activation patterns seen with recovery genuinely reflect adaptive cortical reorganisation. This issue will be discussed further in the conclusions to Section 7 in the light of results from an experiment investigating the neural correlates of attention to movement.

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